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ON PAIRS OF SPECIES

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(WITH TWELVE FIGURES)

Our growing knowledge of the definiteness of variation makes it desirable that botanists should begin to apply this knowledge to a more detailed study of the relationships of particular species. With this end in view I have endeavored to begin such a study by the examination of the various relationships between pairs of species in the same genus. Every botanist knows numbers of such cases, and it occurred to me that it would be worth while to analyze several such pairs as regards their differential characters, habitats, and distribution, to discover whether any light can be thrown in this way on the probable origin of the species in question. How have these differences arisen in the light of our present views of variation?

Again, various rules of distribution have been proposed, such as JORDAN'S law that related species occupy adjacent areas. It is not the purpose of this paper to discuss questions of distribution at any length, but it will be seen incidentally that a species and its next of kin may occupy (1) the same locations, (2) adjacent areas, or (3) widely separated regions. They may overlap, or the distribution may be practically coterminous. From such facts as these it might appear that JORDAN'S law as applied to plants is more honored in the breach than in the observance; but when applied to the variations or tendencies to variation within the taxonomic species, every botanist knows how usually it holds as modified by

topographical conditions. In passing from east to west or from north to south of the continent, the succession of species often seems to form a graded series, though more or less disturbed and modified by the incidence of mountain ranges, plains, etc., a fact which is relied upon in many ways by systematic botanists in their pursuits.

This preliminary study of the relationships and distribution of pairs of species is perhaps of more value for its suggestiveness than for any direct contribution of facts; at least it is to be hoped that such is the case, for the species I have chosen are all familiar forms in the North American flora. Nevertheless, from the material I have examined in this study it has been necessary to describe several new and hitherto unrecognized varieties, and certain others will be described in another connection.

Notwithstanding the great amount of speculation, and more recently of experimental work, on the factors of evolution, scarcely any attempt has been made hitherto to show how one living wild species has been derived from another particular species, or from the common ancestor of both. No doubt systematists frequently have such questions in mind when delimiting species, but, if the methods of experimental evolution are sound, they should enable us by now to begin the application of the ideas so gained to the solution of simple examples taken from wild nature. Even though the historical relationships of many species must remain obscure, yet there exist cases in which the course of events is simple and to some extent within our present powers of analysis.

The pairs I have chosen have been taken at random. In a subsequent study I may make a more methodical selection. In some instances of species pairs the genus is bitypic; in others the two species may stand apart from the others in the genus, either in their structure or their distribution. Some of the cases of real pairs, however, are not obviously pairs at all, and are only found to be such by a study of their internal structure. On the other hand, some species which form an apparent pair in a given region are not very closely related to each other, and have only become paired through the vicissitudes of altering distributions. Such instances show that the mere taxonomic comparison of species, un-

less supplemented by histological or experimental investigations, may lead to quite erroneous ideas concerning the relationships of the species within a genus. There needs to be developed a taxonomy based upon the anatomical and cytological structure of plants, as well as upon the traditional comparison of their external morphology. This need has often been emphasized, and it appears now to be time to begin to put the principle into practice. If the present paper leads to the closer scrutiny of known species from this aspect its purpose will have been accomplished.

An instructive example of the value of cytology in determining relationships has recently been furnished by *Spiranthes* (*Gyrostachys*) *cernua* (L.) Richard. Reasoning by analogy from the case of *Oenothera gigas*, Miss PACE¹ found that it is a true cell giant, having twice as many chromosomes as *S. gracilis* (Bigel.) Beck, and a corresponding increase in cell size and stature. The two species are shown in fig. 1. *S. cernua* is conspicuously larger in all its parts, having larger flowers, stouter stems, and longer, though usually narrower, leaves.^{1a} There is variation particularly in the length of the spike and the width and shape of the basal leaves.

ANDREWS² observed three distinguishable forms of *S. cernua* in a meadow at Williamstown, Massachusetts. The type is pure white and fragrant. A variety which was the common form in this meadow differed in having cream colored or yellow flowers which were not fragrant, a shorter, broader, and more rounded or 2-lobed lip, and leaves also distinct in shape and structure. A second variety, found in one spot some distance away, was white flowered, but otherwise agreed with the yellow variety. Similar forms are recorded from Manchester, New Hampshire, and from Mount Desert Island, Maine. A var. *ochroleuca* (Rydb.) Ames has also been described, having greenish, cream colored or white flowers, longer floral bracts, growing in dry ground, and blooming somewhat later. The tetraploid *S. cernua* would thus appear

¹ In *S. gracilis* $2x=30$, while in *S. cernua* $2x=60$. PACE, LULA, Two species of *Gyrostachys*. Baylor Univ. Bull. 17. no. 1. pp. 16. figs. 50. 1914.

^{1a} Figures of these species are also found in TORREY, Fl. N.Y. 2: 282. pl. 129. 1843.

² ANDREWS, LEROY, On some variations of *Spiranthes cernua*. Rhodora 1: 110-111. 1899.

to be more variable than other species, such as *S. gracilis* and *S. praecox*. Indeed, it is stated in GRAY'S *Manual* to be "very variable in size and foliage." This is interesting because of the fact that *Oenothera gigas* is also more variable, particularly in foliage, than the other, non-tetraploid, mutants. The increased variation, which is of a remarkable kind in *O. gigas*, is probably concerned with new distributions of the quadruple chromosome series in meiosis.



FIG. 1.—*Spiranthes gracilis* (three plants on the left) and *S. cernua* (plant on the right).

Another interesting feature of *S. cernua*, which apparently has not been reported in the other species of *Spiranthes*, is the prevalence of apogamy and polyembryony. LEAVITT³ found that an abundance of seed is set when fertilization is excluded, and that 1-5 or 6 adventive embryos occur. They vary greatly in shape, from

³ LEAVITT, R. G., Polyembryony in *Spiranthes cernua*. *Rhodora* 2:227-228. 1900.

———, Notes on the embryology of some New England orchids. *Rhodora* 3:61-63, 202-205. *pl.* 33. 1901.

spherical to elongate, irregular, or lobed. In a few plants of this species the embryo sac develops normally, followed by fertilization and the production of embryos, but the embryos always possess an apical protuberance which is lacking in the polyembryonic embryos of apogamous plants. The exact manner of origin of the apogamous embryos was not determined, but it appears that individual plants produce embryos which are either all apogamous or all resulting from fertilization. This matter is worthy of further study. No other orchid is known to exhibit this type of polyembryony, although twin embryos occur in many species; but the latter are believed to result from a doubling of the embryo sac followed by fertilization by two pollen tubes. These facts are of interest because it is known that tetraploid species are frequently apogamous.⁴

It has also been observed⁵ that a peculiar form of vegetative multiplication takes place in *S. cernua*, in which young plants are produced from the root tips, but in this case a similar development was reported by STRASBURGER in *Neottia* sp.

Another interesting point is the manner in which light is thrown on relationships by cytological study. The mutation theory is destined in this way to modify many current taxonomic conceptions of relationship. *Spiranthes cernua* in the manuals is separated from *S. gracilis* by several other species, yet it must have been derived at some time from this or possibly from one of the other diploid species. It is even possible, as Miss PACE suggests, that *S. cernua* may still be arising by sporadic mutations from *S. gracilis*. Both species have much the same range, from Nova Scotia to Manitoba, Florida, and Texas. The borders of distribution of this pair of species are nearly, if not quite, coterminous.

CLINTONIA BOREALIS (AIT.) RAF. AND *C. UMBELLULATA*
(MICHX.) TORR.

As regards distribution, *Clintonia borealis* is more northerly and much more widely distributed than *C. umbellulata*. It occurs

⁴ See GATES, R. RUGGLES, *The mutation factor in evolution*. London: MacMillan and Co. 1915 (pp. 197 ff.).

⁵ HALL, J. G., *Vegetative reproduction in Spiranthes cernua*. *Rhodora* 7:49-50. fig. 1. 1905.

from Newfoundland to Minnesota, and south in the mountains to North Carolina. *C. umbellulata*, on the other hand, is confined to the region from New York to Georgia and Tennessee. A comparison of the species shows the following differences:

| <i>C. borealis</i> ⁶ (fig. 2) | <i>C. umbellulata</i> (fig. 3) |
|---|---|
| Scape 1.5-4 dm. high | Scape 2-4.5 dm. high |
| Umbel 3-6-flowered, pedicels stouter | Umbel several to many-flowered, pedicels shorter, pubescent |
| Flowers greenish-yellow, 8-10" long | Flowers white, odorous, often purple dotted, 4-5" long |
| Ovules numerous, in 2 rows in each cavity | Ovules 2 in each cavity |
| Berry oval, several-seeded | Berry globose, few-seeded |

There is apparently no constant difference in the foliage or pubescence, though *C. umbellulata* frequently has larger leaves and is usually more pubescent. *C. umbellulata* has, on the average, a somewhat taller scape; its flowers are more numerous but only half as large as in *C. borealis*; the pedicels are also shorter, more slender, and more pubescent, and the ovules and seeds fewer. In both species the leaves have ciliate margins. In *C. borealis* the scape is nearly glabrous, the pedicels more pubescent; in *C. umbellulata* the scape is pubescent and the pedicels densely so. Summing up the differences, we find them chiefly quantitative, and yet the species do not overlap and there is never any difficulty in distinguishing them, unless it be in the region where they both occur. Here it is possible that there may be intercrossing, giving rise to intermediate forms; but it seems clear, as BATESON⁷ has pointed out in similar cases, that such intermediates are, at least in many instances, secondary and not primary in origin. They appear where the two species come in contact, and result from crossing rather than from original variations.

Although *C. umbellulata* averages larger in size, its flowers are conspicuously smaller, and white in color. It is evident that all

⁶ In drawing up the contrasting characters I have frequently consulted GRAY'S *Manual* and BRITTON and BROWN'S *Flora*.

⁷ BATESON, WM., *Problems of genetics*. p. 158 and elsewhere. Yale University Press. 1913.

of these changes could not have arisen through a single mutation, so it becomes necessary to postulate a common ancestor for the two species. Such an ancestor we may suppose threw off a series of



FIG. 2.—*Clintonia borealis* (Ait.) Raf.

mutations which again continued to mutate in new directions, as we know to happen in other forms from genetic experiments. The surviving forms which we now know as *C. borealis* and *C. umbellulata* might easily represent a differential of not more than three or



FIG. 3.—*Clintonia umbellulata* (Michx.) Torr.

four mutations. The various other mutants and combinations we may suppose to have been eliminated by selection or by their own instability. The fact that *C. umbellulata* is odorous, while *C. borealis* has no marked odor, is by no means unique. Similar cases occur in various other genera, including *Oenothera* and the variation in *Spiranthes cernua* recently mentioned. They find their parallel and no doubt their basis in organic chemistry, where a change of an atom or even a rearrangement of the atoms in a molecule produces an odorous compound from an odorless one.

STREPTOPUS AMPLEXIFOLIUS (L.) DC. AND *S. ROSEUS* MICHX.

In comparing these well known species we find a more marked series of differences. As regards distribution, *S. amplexifolius* is boreal and circumpolar, occurring in Europe and Northern Asia, Greenland, Newfoundland, Labrador to Alaska, and south to North Carolina and California. *S. roseus* is not found in Europe or Asia, but occurs from Newfoundland and Labrador to Alaska, and southward to North Carolina and Oregon.

FERNALD⁸ has made a careful study of the differences between the two species, which may be briefly set forth as follows:

| <i>S. amplexifolius</i> (fig. 4) | <i>S. roseus</i> (fig. 5) |
|--|---|
| Stem whitish and glabrous above | Stem greenish and usually ciliate-hispid above |
| Leaves strongly glaucous, amplexicaul, glabrous | Leaves green, scarcely amplexicaul, conspicuously ciliate |
| Perianth segments spreading widely and quickly recurved | Perianth segments slightly divergent, only the tips becoming recurved |
| Anthers lance-subulate, entire, many times longer than the filaments | Anthers narrow-ovate, bifid, about the length of the filaments |
| Stigma subentire or merely shallow-lobed | Stigma deeply 3-cleft |

These two common and widespread species thus exhibit a number of conspicuous unit differences, which are unlike the differences in the pair of species of *Clintonia* previously examined. The

⁸ FERNALD, M. L., The genus *Streptopus* in eastern America. *Rhodora* 8:69-71. 1906.



FIG. 4.—*Streptopus amplexifolius* (L.) DC.

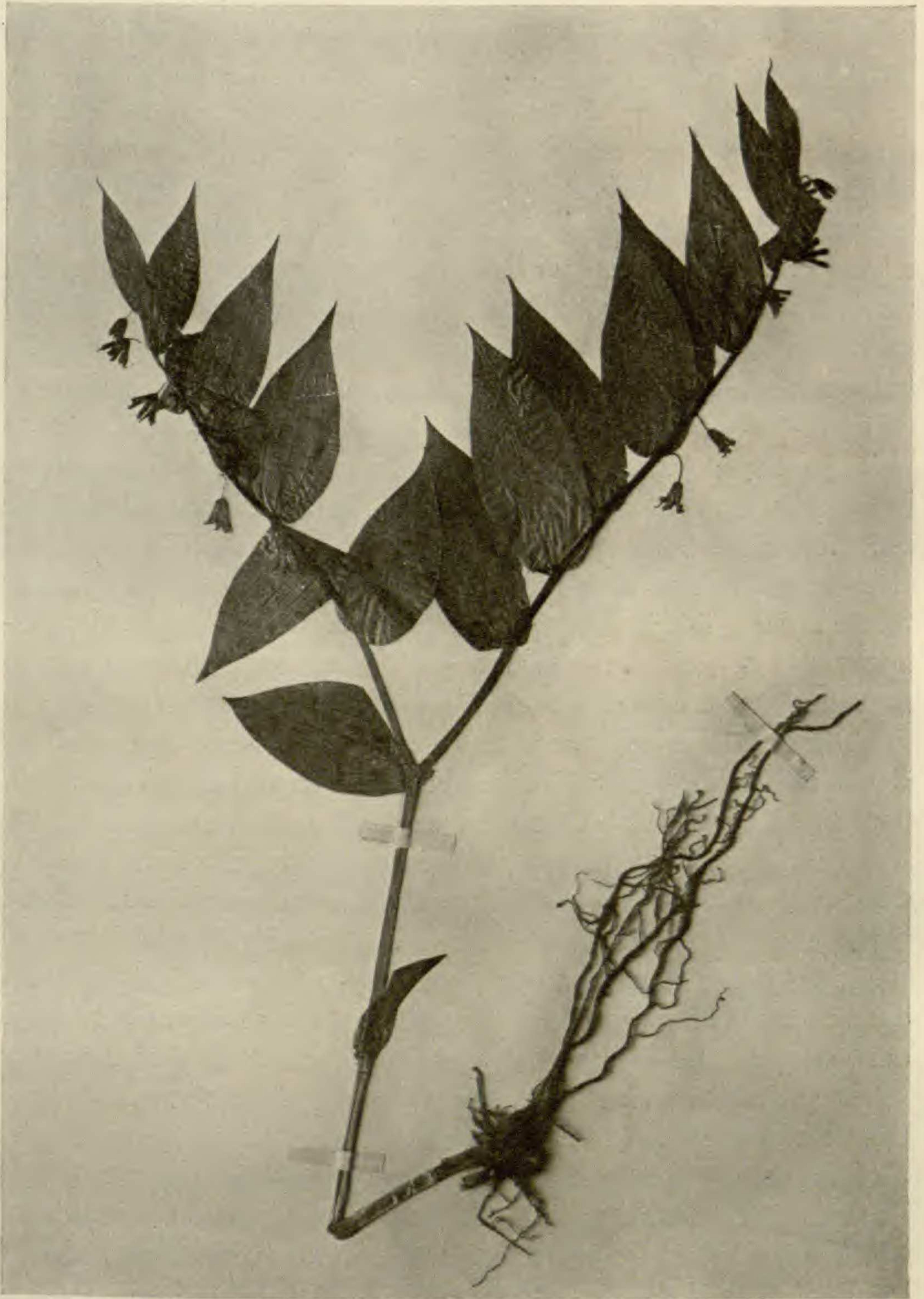


FIG. 5.—*Streptopus roseus* Michx.

most conspicuous of these differences would appear to be probably quite independent of each other, and we cannot imagine them all having originated at one stroke. Thus, the leaves of one are (1) glaucous and amplexicaul, of the other beautifully ciliate; (2) the perianth segments of one are widely spreading and recurved, of the other campanulate; (3) the anthers of the one are entire on long filaments, of the other forked and on short filaments; (4) the stigma of the one is nearly entire, of the other 3-cleft. These four main differences are probably not correlated with each other, and may have originated through several independent changes in the common ancestor. This hypothetical ancestor we may suppose threw off a series of new forms differing from each other in various unit characters, just as mutations are known to occur in *Oenothera*, *Drosophila*, and other genera today. The forms exhibiting these unit differences intercrossed, and, certain of the resulting combinations proving more stable than others, two of the more extreme combinations finally survived, while the others gradually disappeared. This is of course only one of the possible hypotheses to account for the occurrence of two such species.

A hybrid between these two species has been described by FERNALD⁹ from the Gaspé Peninsula under the name of *S. oreopolus*. This form has leaves less ciliate than in *S. roseus*, and flowers like those of *S. amplexifolius* but deep claret-purple in color. There is thus some evidence that the various character differences do behave independently of each other, and it is also a significant fact that the hybrids are sterile. In this connection I should like to point out the possibility that the elimination of intermediate unit steps between such species as these may be due not only to the instability of certain combinations (since they would split in their offspring), but to the sterility of certain combinations; or, in other words, their inability to produce any offspring. There is evidence, which I need not detail here, to show that sterility in crosses is a condition which may originate relatively suddenly in connection with a series of mutations. In other words, sterility has probably not arisen gradually as the species became farther differentiated, but certain forms are doomed to be sterile with certain other forms

⁹ FERNALD, M. L., *Rhodora* 8:70. 1906; 9:106. 1907.

from the moment of their origin, just as certain chemicals will react with each other while others will not.

It seems highly improbable that the specific differences between *S. amplexifolius* and *S. roseus* are directly of selective value to their possessors. We are beginning to learn that natural selection must often act in more roundabout ways, through sterility, etc., and not directly as arbitrator between the possessors of one or other of a pair of differential characters. The character differences themselves must often be innocuous as regards the economy of the plant.

MAIANTHEMUM DILATATUM (WOOD) NELSON AND MACBRIDE¹⁰
AND *M. CANADENSE* DESF.

The genus *Maianthemum* has been variously considered as having one, two, or three species. *M. bifolia* DC. in Europe and *M. canadense* Desf. in North America are now regarded as distinct, and a giant form variously known as var. *kamtschaticum* Gmel. and var. *dilatatum* Wood has been attached to the former species. It is clear that *M. bifolium* and *M. canadense* are distinct, and there seems no doubt that this "variety" should be recognized as a third species. NUTTALL first recognized it as such. It is found in Western America, from California northward to Alaska, and apparently in adjacent Asia.

This species is essentially a giant *M. canadense* except that the leaves have nearly the peculiar shape of *M. bifolium*. In view of our knowledge of the relation between *Oenothera Lamarckiana* and *O. gigas*, it would not be at all surprising if this also proved to be tetraploid. It is to be hoped that some one will make a cytological comparison of these two species. Their differences are shown in fig. 6. *M. dilatatum* is not only stouter, with larger inflorescence and larger leaves, but the leaves also differ in shape, being broader and with conspicuous basal lobes. This is not at all incompatible with tetraploidy, as we know from the case of *Oenothera gigas*, in which the leaves are very much broader and obtuse pointed.

¹⁰ *Maianthemum dilatatum* (Wood) Nelson and Macbride, BOT. GAZ. 61:30. 1916. *Maianthemum bifolium* var. *dilatatum* Wood, Proc. Acad. Phila. 1868: 174; *Smilacina dilatata* Nutt. ex Baker, Jour. Linn. Soc. 14:563. 1875; *Convallaria bifolia* var. *kamtschaticum* Gmel. Cham. and Schlecht. Linnaea 6:587. 1831.

In the examination of a considerable amount of herbarium material, I have seen no intermediates between *M. dilatatum* and *M. canadense* or *M. bifolium*, although even if such occur it by no means diminishes the possibility that *M. dilatatum* originated from *M. bifolium* or *M. canadense* through a single mutation, for when *O. gigas* crosses with *O. Lamarckiana*, intermediate hybrids are



FIG. 6.—*Maianthemum canadense* Desf. (on the left) and *M. dilatatum* (Wood) Nelson and Macbride (on the right; a portion of one leaf was accidentally broken in taking the photograph).

produced, and these again when crossed back with either parent species produce new intermediate stages. *O. gigas* is also very variable in foliage, probably as a result of the tetraploid condition. If these two classes of variants were found in a population of typical wild *O. gigas* and *O. Lamarckiana*, they would prove very confusing from the systematic point of view, but from the genetic

standpoint their occurrence in no way obscures the relationship of the two species; and the same is true of all other tetraploid species when they come to be known as such.

There seems to be a tacit recognition of *M. dilatatum* as peculiarly related to one of the other species, for it has been classed as a variety, although it is easily as distinct from either *M. bifolium* or *M. canadense* as these are from each other.

If this supposition with regard to this pair of species of *Maianthemum* proves to be correct, then their relationship to each other is very different from that found in our pairs of *Clintonia* or of *Streptopus*, for in the latter cases we found it necessary to assume that pairs had arisen through several divergent steps, accompanied no doubt by free intercrossing of the various forms produced by these successive mutations. In *Maianthemum*, however, we assume one species to have given rise directly to the other, and any intermediates to have arisen later through crossing.

The specimens of *M. dilatatum* examined show little variation in foliage, and this may perhaps be taken as an indication that the species is not tetraploid, although in any case its cells may be expected to be conspicuously larger than in *M. bifolium* or *M. canadense*.¹¹ Since its leaf shape agrees with that of *M. bifolium*, it is probably best considered as a giant of that species, although it agrees with *M. canadense* in being glabrous. *M. dilatatum* thus bears features of both the other species, although it is entirely distinct from either. We may reasonably assume that it originated from a glabrous variety of *M. bifolium*, which had itself arisen from the type through a negative mutation in loss of pubescence.

RANUNCULUS ABORTIVUS L. AND R. ALLEGHENIENSIS BRITT.

My attention was directed to this pair of species by Dr. J. M. GREENMAN. *R. abortivus* has much the wider range, occurring from Labrador and Nova Scotia to Manitoba, and south to Florida, Arkansas, and Colorado; while *R. allegheniensis*, a segregate

¹¹ Unless, perchance, it is not a cell giant at all. The well known frequency with which Pacific coast species are conspicuously larger than their more eastern congeners makes one doubt the possibility that they are all cell giants. Their greater vigor may result perhaps from an effect of climate. Only a cytological examination can determine these matters.

described by BRITTON, has been found only from Vermont, eastern Massachusetts, and New York to the mountains of North Carolina. The relative distribution of these species is similar to that of the species of *Clintonia* previously considered, although in this case *R. allegheniensis* occurs wholly within the range of the other species. The specific differences may be tabulated as follows:

| <i>R. abortivus</i> Linn. | <i>R. allegheniensis</i> Britton |
|---|--|
| Stem leaves divided into oblong or linear, somewhat cuneate lobes | Stem leaves divided into linear acute segments |
| Petals pale yellow, shorter than the small reflexed calyx | Stem glaucous |
| Styles very short, curved | Petals pale yellow, minute |
| | Styles subulate, hooked, nearly half as long as the achene |

The main distinguishing feature of these two species is the conspicuous recurved beaks of the achenes in *R. allegheniensis*. The other differences are very inconspicuous and in themselves scarcely noticeable. It seems reasonable to suppose that this species has arisen from *R. abortivus* through a single positive mutation. The idea that these conspicuous beaks might have been gradually developed through natural selection might have been readily accepted at the end of the last century, but has since lost its plausibility. All the facts, both of characters and distribution, are more reasonably explained on the mutation hypothesis. An increased length of beak is, so far as I know, of no considerable use to the plant, although it is possible that the large hook might aid the seeds in transportation by attachment to animals. In distribution, however, the plant, while locally abundant, is restricted in area, and *R. abortivus* surrounds it on all sides except where they both reach the Atlantic coast. This points, not to its having an advantage over *R. abortivus* in the struggle for existence, but more probably to its having originated from that species relatively recently through a mutation, and having since propagated itself and spread with no conspicuous advantage or disadvantage in competition with the parent form.

The wide northerly distribution of *R. abortivus* makes it appear probable that it is the older species and has given rise to *R. alle-*

gheniensis. Only if the distributions were reversed would it appear probable that *R. allegheniensis* had given rise to *R. abortivus*, through a negative mutation in the nearly complete loss of the beak.

ACTAEA ALBA (L.) MILL. AND A. RUBRA (AIT.) WILLD.

In the genus *Actaea* the species are all remarkably similar in foliage and habit, almost the only sharply contrasting characters being found in the thickness of the pedicels and the color of the berries. All the American forms were formerly treated as varieties of the European *A. spicata* L., but it has become customary to treat them as species. *A. alba* and *A. rubra* constitute a conspicuous pair of these species in eastern North America. They have both been considered varieties of *A. spicata*, but are no doubt worthy of specific recognition. We may first compare them, and then we shall find it profitable to examine the whole genus *Actaea*.

| | |
|--|---|
| <i>Actaea alba</i> (L.) Mill. (fig. 7) | <i>Actaea rubra</i> (Ait.) Willd. (fig. 8) |
| Leaflets generally more incised, teeth and lobes acute or acuminate | Leaflets ovate, or the terminal one ovate, toothed or somewhat cleft, the teeth mainly rounded or mucronate, or acutish |
| Raceme oblong | Raceme ovoid |
| Petals truncate, slender, like transformed stamens | Petals rhombic-spatulate, much shorter than the stamens |
| Fruiting pedicels thick | Fruiting pedicels slender |
| Berries ellipsoid (globular-ovoid, Gray's <i>Manual</i>), white often with a purplish spot at the end | Berries oval (ovoid-ellipsoid, Gray's <i>Manual</i>), red |
| Flowering a week or two later | |
| More common westward and southwestward | |
| N.S. and Anticosti to Ga., west to Minn. and La. | N.S. to N.J. and Pa., west to S.Dak. and Neb.; also Idaho |

A. rubra varies in foliage from forms scarcely if at all distinguishable from the typical *A. spicata*, to forms having larger, coarsely

serrate, and less pointed leaves; but the European *A. spicata* L. shows a very similar series of variations, so it is very doubtful if

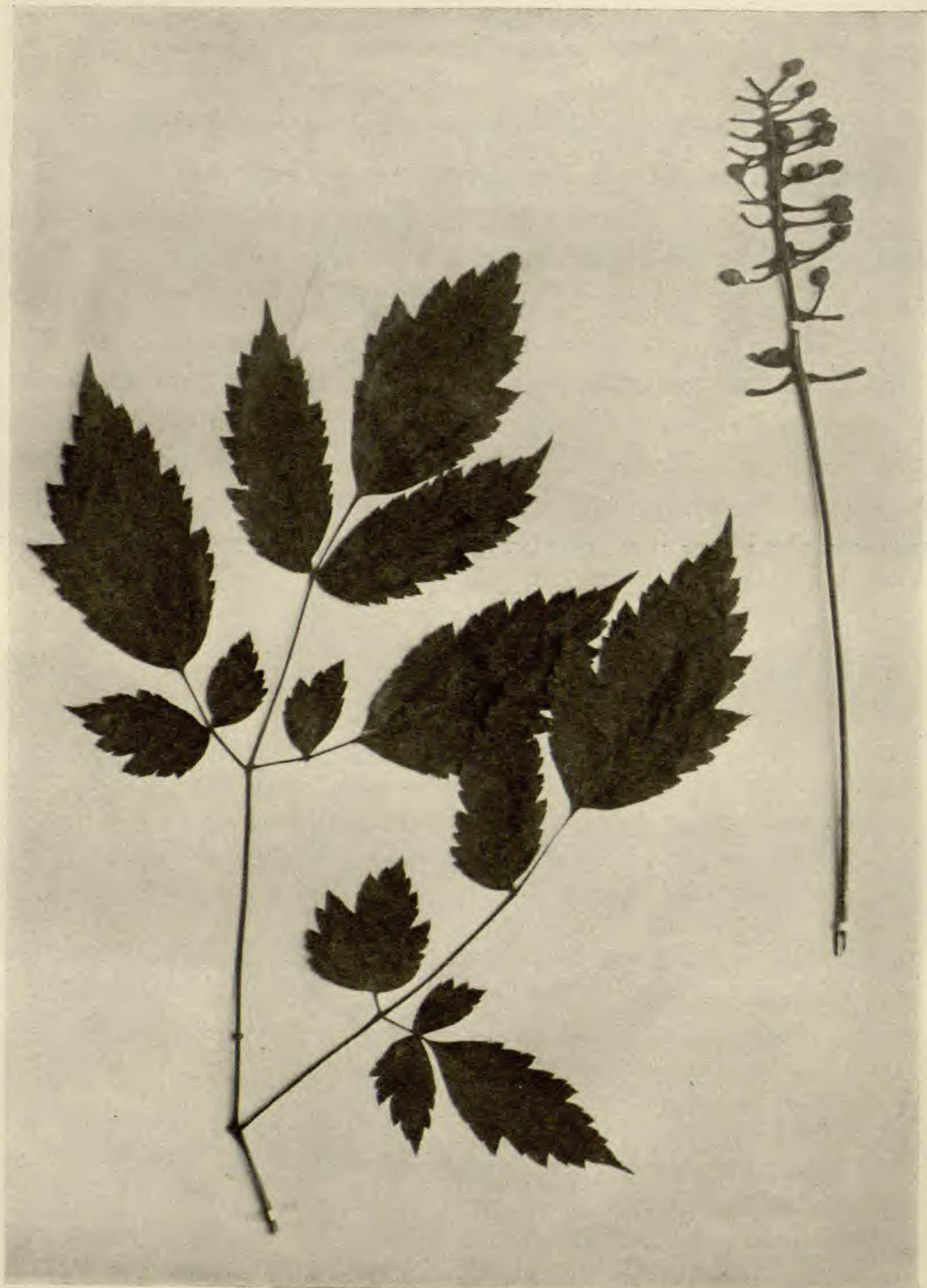


FIG. 7.—*Actaea alba* (L.) Mill.

there is any constant distinction between these species in foliage. The same must be said of *A. rubra* and *A. alba*. The conspicuous

differences between these species are two: (1) the berries red or white, (2) the pedicels in fruit slender or stout. The latter differ-



FIG. 8.—*Actaea rubra* (Ait.) Willd.

ence is clearly shown in figs. 7 and 8, which also show the great similarity in foliage.

As we shall see, several of the species may produce either white- or red-berried individuals, while the pedicels remain slender, so

that the color of the fruits and the thickness of the pedicels are independent pairs of unit characters, and we may consider *A. alba* as perhaps having originated from *A. rubra* through two mutations, in one of which the chief change was in the color of the berry, while in the other it was in the thickening of the pedicels. If there are two Mendelian pairs here, however, it is difficult to see why the two combination types, (1) white berries and thin pedicels and (2) red berries and thick pedicels, are not of more frequent occurrence. Crossing experiments, if they could be carried out, would doubtless throw light on the situation and would be of very great interest. Red berries perhaps would be dominant over white berries, but since a red tip remains to some at least of the white berries, the white may be dominant and the plants with red-tipped berries heterozygous. Whether there would be any dominance of slender or thick pedicels is impossible to say.

A more careful analysis, however, discloses other differences besides those mentioned. Thus LLOYD¹² describes the differences between the fruits of *A. rubra* and *A. alba* as follows: *A. alba* has its fruit (1) on thickened pedicels, (2) smaller, (3) with a larger tip, (4) with a much thicker "integument," (5) without pulp, (6) with larger and fewer seeds (6 instead of about 12), whose sides are more slanting and their surface smooth (not roughened). They also cite observations of Mrs. STOWELL, who found that in *A. alba* the pedicels were much harder, firmer, and darker, and with much larger starch grains.¹³ These authors cite the occasional occurrence

¹² LLOYD, J. U. and C. G., *Drugs and medicines of North America*. 1884-1885 (p. 232).

¹³ Hand sections of the pedicels from dried material of these two species show that she failed to note the essential differences. The ring of wood is the same in structure and diameter in both cases, but in *A. alba* the pith fills the center, while in *A. rubra* it contains an irregular cavity frequently extending as a slit across the diameter of the xylem ring. The increase in thickness of the pedicel in *A. alba* is due to the much greater thickness of the cortical tissue, which is composed of about 7 rows of enormously larger cells than in *A. rubra*. In the latter not only are these cells very much smaller, but the number of rows of cells is only 3 or 4. No differences in the size or shape of the starch grains in the two species were observed, but the large cells in the cortex of *A. alba* contain a great amount of starch, while the small cells of *A. rubra* contain very little. With these structural differences, it might be supposed that the pedicels of *A. alba* would be less firm and rigid than those of *A. rubra*. This point should receive further study.

of plants having white berries on slender pedicels or red berries on thick pedicels, and give it as their opinion that such forms are sports and not hybrids.

MERRIAM¹⁴ has also made observations on the differences between these two species. He found that *A. rubra* has very delicate green pedicels, three-quarters of an inch in length, and berries a half larger than *A. alba*, the pedicels being *hollow*, so that they are easily crushed between thumb and finger. In *A. alba* the pedicels are very thick, red, half an inch in length, the berries small (one-third inch), the pedicels being *solid* or nearly so and not easily crushed. Sometimes the berries in *A. alba* are red, the difference in color being the only change. This suggests that the white of *A. alba* may be dominant to red.

Earlier observations on these species were made by BIGELOW,¹⁵ who described *A. alba* independently under the same name,¹⁶ not knowing that MILLER had described it previously.¹⁷ He points out several other distinctions between *A. rubra* and *A. alba* in his descriptions, which may be summarized as follows:

| <i>A. alba</i> Bigelow | <i>A. rubra</i> Willd. |
|---|---|
| Stems and leaves somewhat larger and smoother | |
| Raceme oblong, twice the length and half the breadth of <i>A. rubra</i> | Raceme hemispherical or half ovate |
| Pubescence of peduncles and pedicels more sparse than usually occurs in <i>A. rubra</i> | Peduncles round, smooth, slightly pubescent at top |
| Pedicels shorter and thicker | Pedicels pubescent, largest at the extremities |
| Sepals 4, oblong, white, concave, caducous | Sepals 4, oblong, green, striate, concave, caducous |
| Petals 4-8, white, oval, dilated upward, truncated, deciduous | Petals often 8 or 10, white, oval, acute unguiculate, deciduous |
| Filaments as long as the petals | Filaments nearly twice as long as petals |

¹⁴ MERRIAM, J. S., Bull. Torr. Bot. Club 3:43. 1872.

¹⁵ BIGELOW, JACOB, Fl. Boston. 2d ed. 1824 (p. 211).

¹⁶ In EATON, AMOS, Manual of Botany. 3d ed. 1824 (p. 155).

¹⁷ Also RAFINESQUE, C. S., Amer. Monthly Mag. 2:266. 1818.

A. alba Bigelow*A. rubra* Willd.

Berries milk white, tipped with red, smaller, about 8-seeded, on short, red, incrassated pedicels as large as the common peduncle

Berries shining, cherry red, about 16-seeded, on long filiform pedicels, one-fourth as large as the common peduncle

Flowers a week or two later

To the differences mentioned on p. 193 we may add therefore (1) greater pubescence of the raceme in *A. rubra*, and (2) filaments nearly twice as long as in *A. alba*. Differences which I have not verified are (3) berries of *A. rubra* with about twice as many seeds, (4) petals more numerous, and (5) sepals green instead of white.

From these facts it is clear that the differences between *A. rubra* and *A. alba* are numerous and affect the fundamental structure of the plant. It becomes a question whether all of these differences could be determined by only two mutations, and this is a matter on which only breeding experiments can throw any light. Of course, it is possible that the quantitative decrease in the pubescence of *A. alba* may be correlated with the increase in thickness of the pedicels, both being structural expressions of the same inner germinal change. Similarly, it is possible, although perhaps scarcely probable, that such changes as smaller size of berries, lack of pulp, larger and fewer seeds, and truncate petals in *A. alba* are all aspects of the same change which made the berries white. The minor differences in shape of berries and leaves have also to be taken into consideration if they are not mere fluctuations.

The frequent occurrence of such vanishing distinctions as those just mentioned affords one of the main difficulties of taxonomic work, and the presence of the "residua" of characters in superposing one species upon another has been thought to offer serious difficulties in explaining the origin of one species directly from another. A careful examination of known mutations, however, shows that similar conditions occur here. Thus, in *Oenothera brevistylis* the main distinctions from *O. Lamarckiana* are in the very short styles and sepal tips and the misshapen stigmas. But minor differences of a quantitative sort are found throughout the plant, notably in the more obtuse tips to the leaves, a feature which shows quantitative variation in the foliage of each individual.

Hence the occurrence of such minor differences in addition to the conspicuous ones is not a difficulty which requires to be explained by the assumption often tacitly made, namely that inherited environmental effects have led to these slight divergences.

We may now examine briefly the whole genus *Actaea* as it stands at present. Taxonomically considered, the species are as follows:

1. ACTAEA ALBA (L.) Mill.

Actaea spicata var. *alba* L. Sp. Pl. 504. 1753.

Actaea alba Mill. Gard. Dist. ed. 8. 1768; Icon. Corn. Canad. t. 77.

Actaea americana var. *alba* Pursh, Fl. Am. Sept. 1:366. 1814.

Actaea brachypetala var. *alba* DC. Reg. Veg. 1:385. 1818.

Actaea brachypetala var. *microcarpa*¹⁸ DC. Reg. Veg. 1:385. 1818.

Actaea pachypoda Ell. Sketch 2:15. 1824.

Actaea alba Bigelow, Fl. Bost. ed. 2. 211. 1824.

Christophoriana americana Park. Theatr. Bot. 379. 1640.

Christophoriana americana, *racemosa*, *baccis niveis et rubris* Morison, Hist. Univ. Oxon. 8. s.1. t.2. f.7. 1680.

2. ACTAEA RUBRA (Ait.) Willd.

Actaea spicata var. *rubra* Ait. Hort. Kew 2:221. 1789.

Actaea rubra Willd. Enum. Hort. Berol. 561. 1809.

Actaea longipes Spach, Hist. Vég. Phan. 7:388. 1839.

Actaea brachypetala var. *rubra* DC. Reg. Veg. 1:385. 1818.

Actaea americana β *rubra* Pursh, Fl. Am. Sept. 2:367. 1814.

Said by GREENE¹⁹ to differ from the European *A. spicata* L. in that (1) the lowest leaf is inserted high above ground (not radical), and (2) the berries are cherry red, not black. As noted by PURSH and embodied in the name of DECANDOLLE, the American species also has shorter petals, the petals of *A. spicata* L. being as long as the stamens. According to SPACH, however, they are sometimes shorter.

A variety of the European *A. spicata* under the names *A. erythrocarpa* Fisch. and *A. rubra* Ledeb. differs in having red instead of black berries, presumably a simple unit change.

2a. ACTAEA RUBRA DISSECTA Britton, having decomposed leaves and incised leaflets, has been recorded from Lincoln County, Ontario, in BRITTON and BROWN, Ill. Fl. 2:55. 1897.

¹⁸ "Baccis parvis albis subrubellis, pediculis incrassatis." This is apparently the pink-berried form sometimes mentioned.

¹⁹ Pittonia 2:108. 1890.



FIG. 9.—*Actaea rubra* var. *gigantea* Gates

2*b*. ACTAEA RUBRA var. **gigantea**, n. var. (fig. 9).—A forma typica differt, grandior omnibus partibus; caule crasso, 3–4 mm. in diametro; foliolo terminale 10–13 cm. longo, latitudine maximo 6–12 cm., grossē dentato, dentibus ad basin 1 cm. aut plus diametro; subtus rugosē-venoso; pedicellis gracilibus sed quam iis typi crassioribus, 14–20 mm. longis; baccae rubrae, 7–14 mm. longae.

This striking giant variety is represented by several specimens and is very distinct, being much larger and coarser in all its parts. It is not improbably a sporadic tetraploid mutation, and it is to be hoped that some one will examine the size of its cells and the number of its chromosomes in comparison with *A. rubra* when the opportunity offers. To be quite consistent, this should be recognized as a species, but there is some advantage at present in regarding it as a variety of *A. rubra* and so indicating its obvious relationship. It forms with *A. rubra* a "pair of species" (cf. figs. 7 and 8). Of the specimens cited later, one (DODGE, 1896) is considerably smaller in all its parts, and perhaps represents an intermediate hybrid between *gigantea* and *typica*, such as we should expect to find where the forms intercross.

The length of the type specimen of *gigantea* from the base of the peduncle to the tip of the central leaflet is about 28.5 cm., while the corresponding length in typical specimens of *rubra* is about 17.5 cm.

Specimens: *J. Fowler*, Fredericton, New Brunswick, July 20, 1892, Herb. Mo. Bot. Gard., type; *E. L. Sturtevant*, Framingham, Massachusetts, July 8, 1890; *Pammel* and *Ball* 236, Ames, Iowa, August 1896; *Chas. K. Dodge*, near Port Huron, Michigan, August 2, 1896 (in part).

A cultivated specimen from Halle in Herb. Mo. Bot. Gard. indicates that the European *A. spicata* L. also probably has a variety *gigantea*.

Hand sections of the pedicels of *A. rubra* were compared with var. *gigantea*. A series of 21 measurements of cortical cells gave in the former case an average diameter of 7.6 μ . A similar series from var. *gigantea* gave an average of 9.4 μ , from which it would appear that the cells are larger, although the difference is not a conspicuous one.

3. ACTAEA NEGLECTA Gillman, in Lloyd, Drugs and medicines of N.Amer. 235. 1884–1885.

Actaea rubra forma *neglecta* Robinson, Rhodora 10:66. 1908.

The distinctions of this form from *A. alba* are stated by GILLMAN as follows: *pedicels green and slender*, leaves 4-ternately compound, racemes ovate, peduncles longer, berry (white) larger, seeds few (about 4) and much rougher, very slightly grooved. By contrast *A. alba* is said to have thick red pedicels, leaves 3-ternately compound, racemes oblong, peduncles much shorter, berries smaller, seeds more numerous (5–7) and nearly smooth, with deep grooves.

4. ACTAEA ARGUTA Nutt. in Torr. and Gray, Fl. N.Amer. 1:35. 1838.

Actaea spicata var. *arguta* Torr. Pacif. R.R. Rep. 4:63. 1856.

Actaea rubra var. *arguta* Greene, Pittonia 2:108. 1890.

Actaea californica Greene, Ottawa Nat. 16:36. 1902.

This western species differs from *A. rubra* chiefly in (1) being larger and stouter, (2) having spherical berries; the leaves are also less divided. Its distribution is from British Columbia to Montana, Idaho, the Black Hills of South Dakota, New Mexico, and California.

A. californica Greene is stated to be very distinct from *A. arguta* Nutt. in its "rhombic ovate acute petals (commonly 3 or 4), its peculiarly broad and almost obtuse leaflets, which are also not much incised," stems often several from the same rootstock as in *A. viridiflora* Greene. The description is inadequate to determine the characters.

So far as can be judged from specimens, *A. arguta* is not so large or stout as *A. rubra* var. *gigantea*.

4a. ACTAEA ARGUTA var. EBURNEA Ckll. in Daniels, Fl. Boulder, Colorado. 119. 1911.

Actaea eburnea Rydb. Mem. N.Y. Bot. Gard. 1:153. 1900.

A. eburnea was described by RYDBERG from Montana. It closely resembles *A. rubra* in size and form of fruit (ellipsoid, 9-12 mm. × 6 mm.) and the form of petals, but the berries are perfectly white, the plant taller, leaflets broader and more acuminate, and the teeth sharper. It is nearer to *A. arguta* in habit, but differs in color and size of fruit and somewhat in the form of the petals. The berries are about 12-seeded, the seeds obliquely pear-shaped, triangular with a rounded back. Its distribution is given as Idaho and Utah to the Black Hills of South Dakota, and also on Mount Mackay, Ontario, and Willoughby Mountains, Vermont. The relationships of this form require further study.

4b. ACTAEA ARGUTA var. ALABASTRINA Lunell, Am. Midland Nat. 2:123. 1911. North Dakota.

This variety has berries spherical or subspherical, 8-10 mm. in diameter, differing from *A. arguta* only in color. Apparently it occurs sporadically. It is possible that *A. eburnea* with ellipsoidal berries should be classed with *A. neglecta*. It differs from var. *alabastrina* in the shape of the berries.

4c. ACTAEA ARGUTA var. **pauciflora**, n. var.—A forma typica decedit, foliorum supra rarē et minutissimē pilosa; inflorescentia 3-4-florā, bracteis obsoletis, petalis duo ellipticis, paulatim in unguiculam abientibus.

Plant large, leaflets 6.5 cm. long, 4-5.5 cm. broad, ovate to oblong, often obscurely 3-lobed, acuminate, rather coarsely incised-dentate, not caudate, upper surface sprinkled with minute shining hairs as in *A. caudata*, lower surface almost completely glabrous except for sparse minute hairs along the main veins; inflorescence composed of only 3 or 4 flowers on short slender pedicels 3-5 mm. long, bracts very small and inconspicuous; petals 2 on the flowers observed, blade elliptic, passing gradually into a claw of nearly equal length reaching nearly to the ends of the filaments; stamens 3-6 mm. in length; pedicels and upper part of peduncle fine pubescent; berries unknown.

Type specimen: *Trelease* and *Saunders*, Harriman Alaska Expedition 3785, Juneau, Alaska, June 8, 1899, Herb. Mo. Bot. Gard.

5. *ACTAEA VIRIDIFLORA* Greene, *Pittonia* 2:108. 1899.

Described from open rocky places, Arizona, in flower July 10, 1889. Since collected in New Mexico (*O. B. Metcalfe* 305, 372) and in southern Colorado (*Baker, Earle, and Tracy* 235). The latter, however, has longer and stouter pedicels²⁰ and is evidently a different thing. The following specimen is also referred to this species: *C. F. Baker* 681, Black Canyon, Colorado, 1901.

This species appears to be well characterized by the following features: (1) stems a cluster from a clump of roots; (2) flowering very late, leaves less developed at time of flowering; (3) racemes reaching 5-6 inches long, particularly narrow, elongated and dense; (4) pedicels all of equal length, shorter (6-13 mm.); and (5) "remarkably short greenish stamens." The petals are said to be "rather numerous," ovate to nearly lanceolate, usually acutish, little shorter than the stamens.

A. viridiflora also occurs in two varieties having respectively red and white berries, but apparently differing in no other particular. The latter might be known as *A. viridiflora* var. *alabastrina*. The white variety presumably originates through a mutation, being found interspersed with the red.

5a. *ACTAEA VIRIDIFLORA* var. **Clementiorum**, n. var.—A forma typica differt, folioliis angustioribus, saepe ad basim cuneatibus; inflorescentiā perbreve et floribus paucioribus; stamina flavis.

This variety would be recognized as a separate species if it were sharply marked off from the type of *A. viridiflora*, but in all characters, except perhaps the color of the stamens, there is a gradual transition series. In the extreme form of the variety the leaves are much divided, and both the terminal and lateral leaflets are for the most part cuneate at base, the teeth serrate. The terminal leaflet is 5-6 cm. in length and 12-30 mm. in width at the widest part.

²⁰ The flowering pedicels are longer and not so stout as in *A. alba*. All other known forms have slender pedicels.

The inflorescence is short (15–35 mm.) and narrow, pedicels short (5–10 mm.) and slender, densely pubescent in anthesis. The petals number about 4, very broadly ovate, sharply narrowed to a claw of equal length; stamens yellow, short but exceeding the petals. These differences may be summarized as follows: (1) leaves highly decomposed, the leaf segments narrower, often cuneate at base, (2) raceme short, containing fewer flowers, (3) stamens yellow.

Specimens: *F. E. and E. S. Clements* 239, Jack Brook, Colorado, June 20, 1901 (two sheets; fruit red), Herb. Mo. Bot. Gard., *type*; *C. F. Baker* 318, near Pagosa Peak, Colorado, August 1899, fruit white.

A photograph of the Jack Brook Station by CLEMENTS shows a dense group of the plants, so that several stems probably arise from one rootstock, as in *A. viridiflora*. The racemes in this group vary considerably in length and most of them bear white berries, but in a few the berries are red. Evidently there is free intercrossing of the type and the variety in Colorado, with blending in foliage and length of raceme, while the red and white berries form a sharply alternating character.

6. *ACTAEA CAUDATA* Greene, *Ottawa Nat.* 16: 35. 1902.

Described from Chilliwack Valley, British Columbia (*J. M. Macoun* 33550 in part). This species is insufficiently known and needs further study. *A. caudata* seems to be chiefly characterized by (1) young petioles and leaflets minutely villous, the latter along the veins beneath; (2) upper face sprinkled with minute, rigid shining appressed hairs; (3) leaflets with a long lance-linear perfectly entire acumination; (4) petals 2 or more, two-thirds the length of the stamens, blade elliptic with a flattened claw of the same length. The berries are unknown.

Specimen: *Shaw*, *Selkirk Flora*, 279. 1904.

7. *ACTAEA ASPLENIFOLIA* Greene, *Ottawa Nat.* 16: 35. 1902.

Described from Yakutat Bay, Alaska (*Funston* 14, 1892), and another specimen collected in Alaska by *A. W. Gorman*. It agrees closely with *A. caudata* in the pubescence of leaves and stems, the caudate tips to the leaflets,²¹ and the presence of usually two petals. The main distinguishing features are (1) leaflets deltoid-lanceolate, incisely lobed to a greater degree than in other species, the lobes serrate; (2) raceme very short and few-flowered; (3) petals less than half the length of stamens, blade round-obovate or almost orbicular, claw equally short.

Specimens: *Trelease and Saunders*, *Harrison Alaska Expedition* 3786, Yakutat Bay, Alaska, June 20, 1899; *E. C. Smith*, *Seattle, Washington*, April 23, 1889; *Mrs. Moore*, *Montana*, 1894;²² *Frank H. Lamb* 1353, Baldy

²¹ This feature is apparently not constant.

²² This specimen has a larger inflorescence than the type, and the leaf tips are not caudate.

Peak, Chehalis County, Washington, 3500 ft. elevation, July 24, 1897;²³ *G. E. Coghill* 151, Pecos River, T.R., New Mexico, August 5, 1898;²⁴ *Fendler* 12, New Mexico, 1847.²⁴

It seems obvious that in studying the species of such a genus as *Actaea* the variations which lead from one species to another have, at least in many cases, not been gradual or continuous, but definite and in certain well defined directions. It seems clear that the nature of these variations has been determined by the internal structure of the germ plasm, the environment acting for the most part merely as a releasing stimulus.

SPIRAEA TOMENTOSA L. AND S. ALBA DUROI

Spiraea alba DuRoi²⁵ (fig. 11) is better known under the name of the European species *S. salicifolia* L. It has a diagonal distribution across North America from North Carolina, New York, and Ontario to Saskatchewan, Iowa, and Missouri, and is also found in Siberia. The members of this pair of species are evidently much less closely related than in the other pairs I have mentioned. Fossil predecessors of *S. tomentosa* (fig. 10) show that the tomentose group of species has long been separated from the non-tomentose group. In other words, the characteristic tomentum on the ventral leaf surfaces appeared in these forms long ago, and heredity has handed it down since that time. It is only the accident of distribution, therefore, that makes *S. tomentosa* and *S. alba* a pair. Indeed, we could better consider the group a trio, for in its more eastern range in the Atlantic states and eastern Canada *S. tomentosa* is paired with *S. latifolia* (Ait.) Borkh. (fig. 12). The latter species is still frequently known under the name *S. salicifolia*. Certain more recent segregates from *S. salicifolia*, such as *S. corymbosa* Raf. and *S. virginiana* Britton, which are more restricted in their distribution, also occupy portions of the range of *S. tomentosa*.

²³ The foliage is transitional to *A. arguta*, but the inflorescence and pubescence agree with *A. asplenifolia*.

²⁴ Resembles *A. asplenifolia* in foliage, but has less pubescence along the veins.

²⁵ *Spiraea alba* DuRoi = *S. salicifolia* var. *alba* Ehr. *S. alba* is distinguished from the European *S. salicifolia* (1) slightly in leaf shape, (2) the inflorescence is a conic not a narrow panicle, (3) the sepals are triangular not ovate, (4) the petals are not pink and are more nearly orbicular.



FIG. 10.—*Spiraea tomentosa* L. var. *rosea* (Raf.) Fernald



FIG. 11.—*Spiraea alba* DuRoi

The range of *S. latifolia* is stated to be from Newfoundland to Saskatchewan, western Pennsylvania, and Virginia. Judging from specimens, the Newfoundland form is probably distinct. *S. tomentosa* occurs from Nova Scotia to Manitoba and south to Arkansas and Georgia. The eastern portion of its range, therefore, is covered by *S. latifolia* and the more western part by *S. alba*.

The present tomentose group is represented by *S. tomentosa*, *S. Douglasii* Hook., and *S. dasyantha* Bge.²⁶ *S. Douglasii* occurs in western America from British Columbia to California. It differs from *S. tomentosa* chiefly in (1) leaves slightly different in shape and serrate only above the middle; (2) tomentum on ventral leaf surfaces always white, never rusty; (3) follicles glabrous, not divergent. *S. dasyantha* occurs in China and Japan. The fossil species *S. Andersoni* Heer, from Alaska, is considered most nearly related to *S. tomentosa*.²⁷ A somewhat variable condition of *S. tomentosa* has been segregated as var. *rosea*.²⁸ It differs from the type in having a less compact inflorescence, and the follicles, though tomentose, are not lanate, becoming glabrate as they mature. The type is generally confined to the coastal plain and the Atlantic states, while this variety is found farther south and west in Wisconsin, West Virginia, and North and South Carolina. The variety merges gradually into the type of the species and the two features, (1) degree of compactness of inflorescence and (2) amount of pubescence on the follicles, appear to vary independently.

S. tomentosa and *S. alba* must then be looked upon as a spurious pair, while either *S. tomentosa* and *S. Douglasii* or *S. alba* and *S. latifolia* constitute real pairs. The tomentose character itself not improbably originated by a step, although it may have increased in amount later. Since *S. tomentosa* and *S. latifolia*

²⁶ RYDBERG (Fl. N.Amer. 22:251. 1908) has described two other "species," *S. tomentosula* from Washington and *S. subcanescens* from South Carolina, both of which are considered to be probably hybrids, the former of *S. Douglasii* and *S. lucida* Dougl., the latter of *S. tomentosa* and *S. alba*.

²⁷ See MAXIMOWICZ, C. J., Adnotationes de Spiraeaceis. Acta Horti Petropol. 6:105-261. 1879.

²⁸ FERNALD, M. L., The inland variety of *Spiraea tomentosa*. Rhodora 14:188-190. 1912. *S. tomentosa* L. var. *rosea* (Raf.) Fernald; Fluk. Alm. 393. pl. 321. fig. 5; RAFINESQUE, New Flora 3:62. 1836.



FIG. 12.—*Spiraea latifolia* (Ait.) Borkh.

occupy much the same habitat, it can scarcely be supposed that the tomentum is a character which determines survival, although of course it is conceivable that a change in its physiology renders necessary this extra protection. Possibly experiments in removing the tomentum from young leaves, if it could be done without injury, might answer this question.

Before leaving this genus I wish to point out a condition in another species of *Spiraea* which can only be supposed to have originated suddenly through a mutation. It is very difficult to conceive a gradual and continuous transition from the foliage of such species of *Spiraea* as we have been considering to that of *S. millefolia* Torr., now known as *Chamaebatiaria millefolium* (Torr.) Maxim., which occurs from Idaho to Arizona and southern California. In this species and the related *C. glutinosa* described by RYDBERG²⁹ from Nevada, the leaves are pinnately divided and the primary divisions are again divided, as in many ferns. Various other features separate this genus from *Spiraea* proper, but the finely bipinnate type of leaf must have been derived from leaves which were nearly entire, and it is easiest to conceive this as having occurred in a few well marked steps. Complete continuity in such a process is out of the question.

Summary and conclusions

In this paper, which is an attempt to apply the concepts of mutation to the practical discrimination of species and the understanding of their relationships, I have selected for consideration several pairs of species and their relatives. It is found that these pairs bear very different relationships to each other, both as regards their characters and their distribution. They may occupy the same territory or adjacent areas, they may overlap, or be widely separated. Again, one species may be a giant of the other, or may differ by a few sharp differences which have probably originated as units, or may show differences which cannot be externally analyzed in this way.

Thus, *Spiranthes cernua* is a tetraploid giant of *S. gracilis* or a related species. *Maianthemum dilatatum* is perhaps a cell giant

²⁹ Fl. N.Amer. 22:258. 1908.

of *M. bifolium*; and *Actaea rubra* var. *gigantea* is probably a cell giant of *A. rubra*, from which it has apparently arisen by a mutation. In the case of *Clintonia borealis* and *C. umbellulata*, the peculiarities of the latter probably represent a differential of three or four definite and independent variations. In this way would arise a series of forms, all of which have been extinguished except the two remaining. This hypothesis differs from the Darwinian theory of natural selection only in assuming that the inherited variations are usually not infinitesimal, but bold and definite strokes. We are merely applying the conceptions gained from the facts of experimental breeding.

The pair *Streptopus amplexifolius* and *S. roseus* presents a similar problem. There are four main pairs of character differences between these species. They may be assumed to have arisen through a series of mutations from a common ancestor. Inter-crossing would lead to various combinations and in some cases blends of these mutant characters. Many such combinations would be gradually eliminated through their own instability or their sterility in producing offspring, leaving finally the present pair of species as survivors. The differences between *Ranunculus abortivus* and *R. allegheniensis* are such that the latter, which is more limited in its distribution, may be reasonably assumed to have arisen from the former through a single positive mutation. It is very difficult, if not impossible, to believe that the conspicuous beak of the achene, which is the main peculiarity of *R. allegheniensis*, could have been developed gradually through natural selection. It is much more probable that the character has no selective value and is merely inherited because it has appeared as a germinal variation.

In *Actaea*, after a somewhat detailed analysis of the differences between *A. rubra* and *A. alba*, it was found desirable to consider the whole genus as it now stands, and incidentally three new varieties were described. The differences between *A. rubra* and *A. alba* are much more numerous than might have been anticipated, yet two mutations are perhaps sufficient to account for the origin of the latter from the former. The thickening of the pedicels in *A. alba* was found to be due to the fact that the rows of cortical cells are

more numerous and the cells themselves enormously larger. The minor differences, as shape of berries and leaves, in which the distinctions are of the vanishing order, are not at variance with the mutation hypothesis, for they are also found when known mutations are compared with their parent forms; for example, in *Oenothera rubrinervis* the foliage characters are not sharply differentiated from those of *O. Lamarckiana*, but are quantitatively separated.

Finally, *Spiraea tomentosa* and *S. alba* constitute a spurious pair of species. In reality *S. tomentosa* is paired with *S. alba* in one part of its distribution and with *S. latifolia* in another part; but *S. tomentosa* has itself been derived from a tomentose ancestor represented by a fossil form from Alaska. Hence its relation to the other two species is more remote, and it only forms a pair with either of them through the accident of their present distribution.

It seems clear that the mutation conception can be applied with advantage to the consideration of all such species relationships, but, of course, crossing experiments and cytological investigations provide the only final answer to the specific questions involved, and it is to be hoped that such investigations will be undertaken, at least in some of the genera discussed in this paper.

The photographs which illustrate this paper were kindly taken by Mr. C. H. THOMPSON. They are all from specimens in the herbarium of the Missouri Botanical Garden, and all specimens cited in this paper are from the same source. I am indebted to the Director, Dr. GEORGE T. MOORE, for the facilities provided for making these observations, and to Dr. J. M. GREENMAN for much kindly help in connection with the work in the herbarium.

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